A dynamic explanation of size–density scaling in carnivores

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Abstract. Population abundance is negatively related to body size for many types of organisms. Despite the ubiquity of size–density scaling relationships, we lack a general understanding of the underlying mechanisms. Although dynamic models suggest that it is possible to predict the intercept and slope of the scaling relationship from prior observations, this has never been empirically attempted. Here we fully parameterize a set of consumer–resource models for mammalian carnivores and successfully predict the size–density scaling relationship for this group without the use of free parameters. All models produced similar predictions, but comparison of nested models indicated that the primary factors generating size–density scaling in mammalian carnivores are prey productivity, predator–prey size ratios, and consumer area of capture.

Key words: abundance; allometry; carnivores; consumer–resource models; macroecology; population dynamics; scaling; size–density relationships.

INTRODUCTION

A widely observed pattern in nature is a negative relationship between body size and long-term mean population density (White et al. 2007). In particular, species drawn from a global or regional pool may show a size–density scaling relationship that takes the form of a power law, $\hat{C} = c_0 M_c^\chi$, where $\hat{C}$ is the average long-term density of consumers, M_c is the mass of the consumer, c_0 is a pre-factor that gives the abundance for a consumer when $M_c = 1$, and χ is a scaling exponent. Size–density scaling relationships occur in diverse groups such as protists (Finlay 2002), insects (Meehan 2006), birds (Russo et al. 2003), and mammals (Damuth 1987).

The density of a consumer population is determined by a dynamic interaction between the consumers and their resources. The parameters that drive this interaction depend on the mass of the consumer, the resource, or both, and these body mass dependencies also may be described by power laws (Yodzis and Innes 1992, Weitz and Levin 2006, Riede et al. 2011). Because consumer–resource models describe this interaction and are built on core processes of births and deaths, they may provide a dynamic and mechanistic explanation for size–density scaling as well as a means to quantitatively predict the scaling for specific groups. Indeed, Weitz and Levin (2006) showed that it is possible for the equilibrium densities predicted by size-dependent consumer–resource models to reproduce −3/4-power size–density scaling, given specific assumptions about how each model parameter scales with the body size of the consumer.

Lacking still is an effort to determine whether consumer–resource models can accurately predict the scaling exponent or pre-factor of any particular relationship. Without this empirical step, we cannot be sure that body-mass-dependent consumer–resource models provide a sufficient explanation for size–density scaling relationships. In addition, because consumer–resource models vary in complexity, without specific quantitative application of this theory and a comparison of different models, we cannot be sure which parameters drive the pattern. Here, we parameterize a set of common consumer–resource models for mammalian carnivores and compare quantitative predictions with the observed size–density scaling observed for this group as shown by Carbone and Gittleman (2002). We find a strong quantitative match between the predicted and observed scaling parameters, and we compare models to identify the processes that generate size–density scaling in this group.

METHODS

We analyzed three body-mass-dependent consumer–resource models that vary in complexity (Tables 1 and 2). The simplest, model 1, is the Lotka-Volterra (LV) model (Lotka 1925). Model 2 adds logistic growth for the resource, and model 3 adds a type II functional response for the consumer (Holling 1959), giving the MacArthur-Rosenzweig model (Rosenzweig and Mac-Arthur 1963), which also was used by Weitz and Levin (2006). We solved each model for the equilibrium consumer density, $\hat{C}$ (Table 2), which is the intersection point of the consumer and resource net zero growth isoclines. In model 1, populations cycle around the equilibrium, whereas in model 2 the equilibrium is always stable. In model 3, both behaviors are possible. Provided that cycles are not of such large amplitude to

TABLE 1. Summary of scaling parameters.

Parameter	Description	Scaling	Data source
C	scaling of consumer density	$c_0 M_c^{\chi}$	Carbone et al. (2007b)
r	maximum population growth rate of resource	$r_0 M_r^{\rho}$	Savage et al. (2004)
K	carrying capacity of resource	$k_0 M_r^{\kappa}$	Damuth (1981)
a	area of capture of consumer	$a_0 M_c^{\alpha}$	Appendix B
e	conversion efficiency of consumer	$e_0 M_c^{\epsilon}$	estimated from a combination of parameters (see *Methods*) and neonate scaling and consumer–resource body size scaling
h	handling time for consumer	$h_0 M_c^{\varphi}$	Appendix B
m	mortality rate of consumer	$m_0 M_c^{\mu}$	McCoy and Gillooly (2008)
M_r	scaling of consumer size with resource size	$s_0 M_c^{\psi}$	Carbone et al. (2007b); Appendix B
N	scaling of neonate size in mammals	$n_0 M_c^{\eta}$	Blueweiss et al. (1978)

Notes: For simplicity, pre-factors are given as lowercase Arabic letters subscripted with 0, and all exponents are given by closest Greek counterparts. See *Methods* for details on parameter estimates.

endanger populations with extinction, the equilibrium provides a reasonable approximation of the long-term mean densities that we aim to predict. By defining body mass scaling functions for each of the models' parameters, we express $\hat{C}$ in terms of the mass of the consumer as a power law (Table 1). Most parameters are directly related to consumer mass, but because prey productivity is related to prey mass, we also include prey size selection in order to express prey productivity in terms of consumer mass.

We estimated the body-size dependence of all parameters with data from the literature (see Table 1 for description of scalings and parameters and Appendix A for estimates of each parameter), focusing on mammalian carnivores preying on mammals. We used the size–density scaling of mammals with the carnivores removed as a proxy for prey carrying capacity, K (Damuth 1987). We used data from Savage et al. (2004) for the scaling of maximum population growth rate, r, using the reported activation energy for metazoans (0.45 eV [~6.602×10^{-19} J]) to temperature-adjust the intercept of the relationship to that appropriate for mammals (~37°C) (Gillooly et al. 2001). We used the supplemental data from McCoy and Gillooly (2008) for mortality rate, m, and the consumer–resource body size data from Carbone et al. (2007b) for the scaling of prey size selection, M_r. We used the neonate data from Blueweiss et al. (1978) in the calculation of efficiency, e (see below).

Previous quantitative assessments of the body-size dependence of functional response parameters (area of capture, a, and handling time, h) are rare and have not been evaluated for mammals. We exhaustively searched the literature for saturating functional response data for mammalian carnivores preying on mammals. To be included, it was necessary that the data were actually presented in a figure so that they could be digitized (see Supplement for raw data), unless parameters were reported in the units required (three cases). The prey data had to be expressed as individuals per area, and a few functional responses could not be used because prey

TABLE 2. Models used in the analysis, the isoclines for both consumer and resource species, and the resultant scaling of equilibrium consumer density.

Equations	Isoclines	Predicted size–density scaling of consumers
Model 1. Lotka-Volterra (LV)		
$\dfrac{dR}{dt} = rR - aRC$	$C = \dfrac{r}{a}$	$\hat{C} = \dfrac{r_0 s_0^{\rho}}{a_0} M_c^{\psi\rho - \alpha}$
$\dfrac{dC}{dt} = eaRC - mC$	$R = \dfrac{m}{ea}$	
Model 2. LV model with logistic growth of prey		
$\dfrac{dR}{dt} = rR\left(1 - \dfrac{R}{K}\right) - aRC$	$C = \dfrac{r}{a}\left(1 - \dfrac{R}{K}\right)$	$\hat{C} = \dfrac{r_0 s_0^{\rho}}{a_0} M_c^{\psi\rho - \alpha}\left(1 - \dfrac{m_0}{e_0 a_0 k_0 s_0^{\kappa}} M_c^{\mu - \epsilon - \alpha - \psi\kappa}\right)$
$\dfrac{dC}{dt} = eaRC - mC$	$R = \dfrac{m}{ea}$	
Model 3. MacArthur-Rosenzweig		
$\dfrac{dR}{dt} = rR\left(1 - \dfrac{R}{K}\right) - \dfrac{aRC}{1 + ahR}$	$C = \dfrac{r}{a}\left(1 - \dfrac{R}{K}\right)(1 + ahR)$	$\hat{C} = \dfrac{r_0 s_0^{\rho}}{a_0} M_c^{\psi\rho - \alpha}\left(1 - \dfrac{m_0}{a_0 k_0 s_0^{\kappa}(e_0 M_c^{\epsilon} - h_0 m_0 M_c^{\varphi + \mu})} M_c^{\mu - \alpha - \psi\kappa}\right)\cdots$
$\dfrac{dC}{dt} = \dfrac{eaRC}{1 + ahR} - mC$	$R = \dfrac{m}{a(e - hm)}$	$\left(1 + \dfrac{h_0 m_0 M_c^{\varphi + \mu}}{e_0 M_c^{\epsilon} - h_0 m_0 M_c^{\varphi + \mu}}\right)$

Note: Parameters and their scaling forms are listed in Table 1.

density was expressed as the number of scats per area. The kill rates had to be expressed as number of individuals killed, and some were expressed as frequencies in scats or as other indices that, to our knowledge, could not be translated into direct kill rates. With these limitations, functional responses for seven species were obtained (Angerbjörn 1989, Zalewski et al. 1995, Turchin and Hanski 1997, O'Donoghue et al. 1998, Stenseth et al. 1998, Eberhard 2000, Sundell et al. 2000, Jost et al. 2005, Nilsen et al. 2009). In order to ensure that all data were normalized to the correct units (kg for mass, days for time, ha for area), we extracted data, normalized units, and conducted regressions to estimate parameters. Two functional response data sets were found for least weasel (*Mustela nivalis*) and wolf (*Canis lupus*), and parameter estimates were averaged. Parameters of the functional responses were obtained by fitting data to a saturating, type II functional response using the curve-fitting tool in MATLAB (MathWorks 2009) (see Appendix B for results of the fitting procedure). The functional response model was $f = (aR)/(1 + ahR)$, where R indicates resource (prey) levels (Holling 1959).

Scaling relationships were estimated using two types of regression. The first, ordinary least squares (OLS) regression, assumes that there is no error in the *x*-variable and assigns all error to the *y*-variable. The second, reduced major axis regression (RMA), assumes that the error is equally divided between the *x*- and *y*- variables. Neither of these assumptions is likely to be true for the data we analyzed. There is error in the estimates of body mass, even for large organisms that can be weighed, because there is a range of body sizes in each population and reported body sizes are not necessarily those that correspond to a particular density. It is also not likely that the body size error is as large as the error in the estimates of functional response, growth rate, or density parameters. Thus, the true scaling exponent lies between that estimated by OLS and RMA. Because there are no established methods that we can use to apportion error in this case (Smith 2009), and because our intent is to find the true relationship between size and several variables, given this intermediate error structure (Sieg et al. 2009), we conducted both regression types and averaged the resulting parameter estimates (OLS, RMA, and average parameters are given in Appendix A). We used log-transformed data in all regressions, which is suitable when data have a multiplicative error structure and proportional changes are of interest, as is the case here (Kerkhoff and Enquist 2009, Xiao et al. 2011).

The 95% confidence intervals (CIs) of the average model parameters were calculated using a bootstrapping procedure. Each data set was randomly sampled with replacement to produce 1000 random data sets of equal size. For each data set, OLS and RMA regressions were conducted, and mean pre-factor and exponent parameters were produced, giving distributions for all parameters. The CIs were taken as the 2.5 and 97.5 percentiles of the parameter distributions (Appendix A). All regressions and bootstrap procedures were conducted in MATLAB (MathWorks 2009).

The efficiency parameter e is the number of predator individuals produced per number of prey individuals consumed. The parameter is really a combined parameter that integrates several steps in the consumption of prey and the production of biomass (DeLong 2011). We can write e more fully as $e = i_g e_p a_p e_r a_e M_r$, where the parameters are, from left to right: the number of individuals produced per gram of production, i_g, which is the inverse of neonate mass (individuals/kg); the efficiency of production, e_p (kg/J); the allocation of energy to production, a_p (no units); the conversion rate of the assimilated mass of resources to energy, e_r (J/kg); the assimilation efficiency, a_e (no units); and the mass of the prey resource, M_r (kg/individual). Given a scaling relationship between M_r and M_c (mass of the consumer), $s_0 M_c^\psi$ (Table 1), and a scaling of neonate mass, N, with adult mass, $n_0 M_c^\eta$ (Table 1), we get

$$e = \frac{1}{n_0 M_c^\eta} e_p a_p e_r a_e s_0 M_c^\psi \quad \text{or} \quad e = \frac{e_p a_p e_r a_e s_0}{n_0} M_c^{\psi - \eta}.$$

Note that in the case of carnivores, $\psi > \eta$, so the efficiency of offspring conversion increases with size. We set $n_0 = 0.05$, $\eta = 0.94$, $s_0 = 0.1$, and $\eta = 1.47$, as estimated (see Table 1 and Appendix A). We set $e_p = 1.6 \times 10^{-4}$ kg/kJ (DeLong et al. 2010) and $e_r = 7000$ kJ/kg (Peters 1983). Assimilation efficiency is set at 0.8 (Moors 1977), and we assume that about 10% of available energy is allocated to biomass production (probably an overestimate). Putting this together, we get a body mass scaling function for e:

$$e = \frac{0.00016 \times 0.1 \times 7000 \times 0.8 \times 0.1}{0.05} M_c^{1.47 - 0.94}$$
$$= 0.17 M_c^{0.53}.$$

Finally, the quantitative prediction for the size–density scaling is produced by plugging in each parameter estimate into the models in Table 2 and calculating the resulting slope and pre-factor. We used a Monte Carlo approach to incorporate error in the scaling relationships of the underlying parameters. Using the bootstrapped distributions of each contributing parameter, we randomly selected 10 000 sets of scaling relationships (pre-factors and exponents were selected as pairs because they are estimated together). These 10 000 sets were used to estimate the distribution of the predicted scaling slope between $\hat{C}$ and M_c, with the 2.5 and 97.5 percentiles representing the 95% CIs of the predicted slope. In addition, we created a vector of carnivore body masses and used the Monte Carlo procedure to produce the 95% prediction intervals for the equilibrium density at each size and plotted these upper and lower intervals along with the mean prediction.

Results

The equilibrium consumer density of model 1 (LV) is a simple ratio of prey productivity and consumer area of

capture (Table 2). Substituting the body mass dependence of these terms, including the body mass dependence of prey size, produces a core expression for size–density scaling:

$$\hat{C} = c_0 M_c^{\psi\rho-\alpha}. \quad (1)$$

Eq. 1 is a power law that includes scaling exponents for prey productivity (ρ), consumer–resource size ratio (ψ), and consumer area of capture (α). The pre-factor is made up of the pre-factors of these contributing variables:

$$c_0 = \frac{r_0 s_0^\rho}{a_0}.$$

Adding resource limitation (logistic growth) and consumer satiation (type II functional response) to get models 2 and 3 adds modifying terms to Eq. 1 (Table 2). Each of these more complex (and presumably more realistic) models adds a term in the form of $(1 \pm x)$, meaning that if the expression x is small, these processes will alter the size density scaling very little. If x is large, they will have an important contribution to the scaling pattern. Only by quantifying each parameter contributing to x can we know the impact of this additional complexity on the size–density scaling.

With data from a range of sources, we estimated all 14 parameters (Appendix A). The scaling of prey density and productivity were very close to previous observations from the original sources. Prey size increased steeply with predator size (Fig. 1A), as expected from previous analyses (Riede et al. 2011). The scalings for mammalian functional response parameters support the assumption that area of capture scales with body mass to the ~3/4 power, in theory due to the necessity of resource acquisition keeping pace with metabolic demand (Yodzis and Innes 1992, Weitz and Levin 2006; Fig. 1B). Although it is logical that handling times should increase with consumer size (Hansen et al. 1997), especially when resource size increases with consumer size, we failed to find a significant relationship (Fig. 1C).

We then made three predictions (one for each model) of the pre-factor and exponent of the size–density scaling for mammalian carnivores (Fig. 2). All models produced nearly identical predictions that closely matched the data, falling within the 95% confidence intervals of the observed size–density scaling (Figs. 2A–C). Given the core expression (Eq. 1), the equilibrium density $\hat{C}$ is predicted to scale with consumer mass as $M_c^{\psi\rho-\alpha} M^{(1.47 \times -0.23) - 0.85} = M^{-1.19}$ (with 95% CIs of -0.79 to -2.91). The additional complexity of models 2 and 3 produced nearly undetectable modifications of this prediction (Fig. 2B, C).

DISCUSSION

Our objective was to determine whether body-size-dependent consumer–resource models, when fully pa-
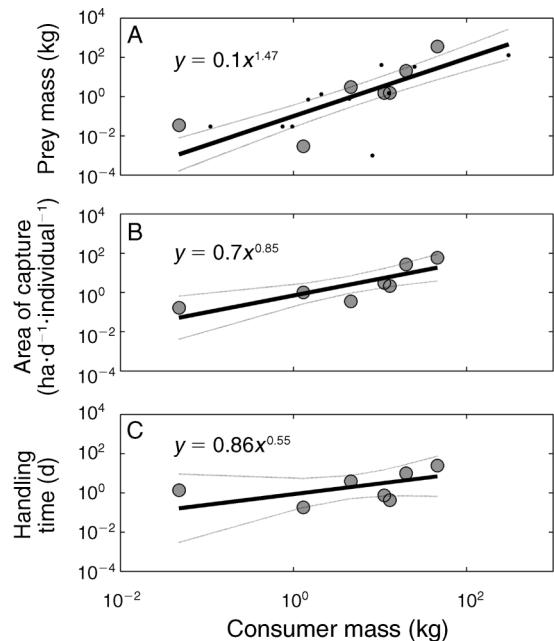

FIG. 1. The scaling of consumption and functional response parameters for mammalian carnivores. (A) Body size of the resource species as a function of consumer body size. The small dots are an additional set of predator–prey body sizes from Carbone et al. (2007b). (B) Dependence of area of capture on consumer size. (C) Scaling of handling time with consumer mass is positive but nonsignificant. Light gray lines show 95% confidence intervals. Large gray circles represent species for which functional response data were available. Estimated scaling relationships are shown (Appendix A).

rameterized using independent data, could quantitatively predict the height (pre-factor) and slope (exponent) of a specific size–density scaling relationship. As shown by Weitz and Levin (2006), the typical $-3/4$-power size–density scaling can be reproduced by these models if certain assumptions about the body mass dependence of the parameters are made. However, without quantitative estimates of the model parameters and a comparison of predicted with observed scalings, it is impossible to say whether this approach produces the correct insight about the mechanisms or to determine which processes are actually important in generating the scaling.

In this study, we produced estimates of all the model parameters and compared predictions from the three nested models to the observed size–density scaling. Our results show a strong match between predicted and observed scaling, confirming that this approach can provide new insights into this long-known, but poorly understood, pattern. We found that size–density scaling in mammalian carnivores depends on the three mass-dependent processes defined in model 1: prey productivity, prey size selection, and predator area of capture. The additional complexity and realism of models 2 and 3 appear unimportant for understanding size–density scaling in this case, although they may play more of a role in other taxa. The reason these additional terms are
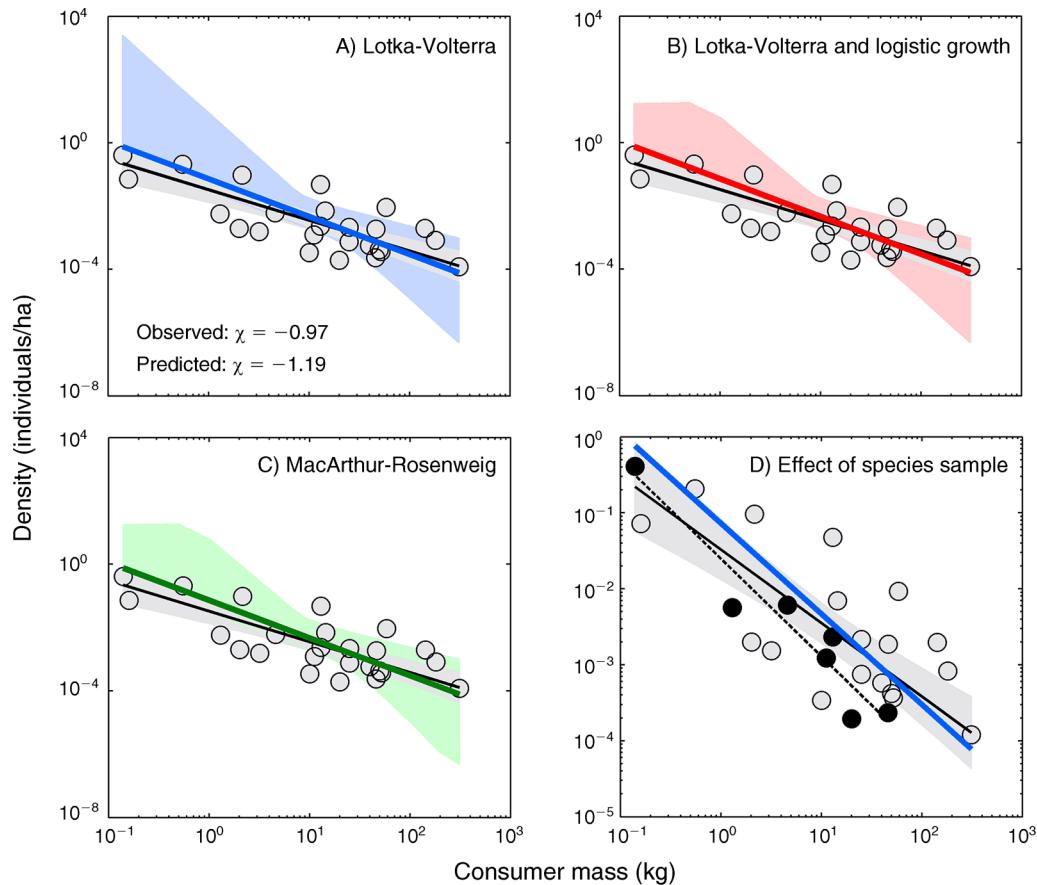
Fig. 2. The size–density scaling of mammalian carnivores is well predicted by simple consumer–resource models. Gray circles show the size–density scaling of carnivores as reported by Carbone and Gittleman (2002). Colored lines are the average fit based on model predictions. The solid black line is the average fit from ordinary least-square and reduced-major-axis regressions, and the gray shaded area is the 95% confidence interval of the overall fit to the data estimated with a bootstrapping procedure (see *Methods*). Panels show predictions for (A) Model 1 (Lotka-Volterra model), (B) Model 2 (Lotka-Volterra model with logistic growth of the prey), and (C) Model 3 (MacArthur-Rosenzweig), with colored areas illustrating the 95% prediction intervals using a Monte Carlo procedure, given the distributions of each contributing parameter. All models produced similar predictions, indicating that only the three major factors in Model 1 are important in determining size–density scaling for this group. In panel (D), the sample of species for which functional response data were available may have affected the predicted slope. The black solid circles represent species for which functional response data were available, and the dashed black line shows an average fit to this subset of the size–density scaling data.

unimportant here is likely because the equilibrium resource densities are lower than their carrying capacities. The observed equilibrium kill rate may occur on or close to the linear portion of the saturating functional response curve, minimizing the difference among models. Reduced resource densities at equilibrium also push growth rates of the resource back up toward r_{max}, reducing the difference between models with and without resource self-limitation. In other words, the isoclines change shape with model complexity, but the intersection point does not change very much.

Carbone and Gittleman (2002) also found that the density of mammalian carnivores scaled with the biomass density of the prey with an exponent of −1.04. We can express this quantity as $\hat{C}/KM_r$ and then rewrite it in terms of a scaling function using the already defined

functions in Table 1:

$$\frac{\hat{C}}{KM_r} = \frac{c_0}{k_0 s_0^{\kappa+1}} M_c^{(\chi - \psi(\kappa+1))}.$$

With the mean parameter estimates for the scaling slopes, we find that the scaling of carnivore density, controlled for prey biomass, is very similar, at −1.1. Thus, the dynamic model captures both the classic size–density scaling pattern as well as the alternative scaling rule controlling for prey biomass. With further within-species detail on variation in functional response parameters, it also may be possible to use this approach to explain within-species variation in population abundance.

It is worth noting that these predictions are made independently of the size–density data (i.e., there are no

fitted parameters), which provides very strong support for our conclusions. However, the slope of the predicted scaling, although statistically indistinguishable from the observed, was slightly steeper than the overall fit, and slightly closer to the observed scaling for the subset of the data (dashed black line in Fig. 2D) for which functional response data were actually available (black circles in Fig. 2D). This suggests that the scaling of area of capture might be shallower if functional responses for species with relatively higher densities could be included. For now, our exhaustive search of the literature suggests that many carnivores are insufficiently studied to be used in this type of analysis.

As a check on the realism of the model, we evaluated whether the individual resource uptake predicted by the model matches the expected energetic demand given by the scaling of metabolic rate. Solving the LV model (we use this because it is the simplest of the three and gives the correct scaling), the equilibrium per capita kill rate is $\hat{f} = m/e$ (DeLong 2011), which when multiplied by the mass of the resource, gives mean per capita biomass consumption rate, $\bar{B}_{ind}$ (assuming all of the mass is eaten, or at least a constant proportion across body sizes). Thus, using our parameter estimates (Appendix A) $\bar{B}_{ind} = (m/e)M_r \propto M^{\mu+\psi-\varepsilon} \propto M^{-0.26+1.47-0.55} \propto M^{0.67}$, (with CIs of 0.64 to 0.71), which is close to and not statistically distinguishable from the observed scaling of metabolic rate in mammals (Sieg et al. 2009). This means that the model, although not invoking metabolic scaling as a constraint, reproduces a realistic scaling of food uptake, and presumably, the ecologically relevant scaling of metabolism as well.

Previous non-dynamic explanations for size–density scaling reside on untested assumptions and have difficulty explaining size–density scaling that deviates from the often-observed $-3/4$ slope. For example, it has been proposed that size–density scaling arises as a kind of "pie-slicing" process (Brown et al. 2004, Marquet et al. 2004). If resource provisioning to a population is independent of body size (Damuth 1981), populations of larger individuals by necessity must be less dense. In scaling terms, maximum consumer abundance, C_{max}, is given by the total amount of resource used by a population, B_{tot}, divided by the average resource used per individual, $\bar{B}_{ind}$. If $B_{tot} \propto M_c^0$ and $\bar{B}_{ind} \propto M_c^{0.75}$, then $C_{max} \propto M_c^{-0.75}$. Although the argument is logical, why total resource provisioning should be independent of consumer size has never been explained or tested (Carbone et al. 2007a). Using our dynamic approach, we can evaluate this assumption and determine whether the pie-slicing model is also an adequate explanation for size–density scaling in carnivores. Defining population-level resource use as the total biomass consumed by the whole consumer population per unit area, we can write $B_{tot} = \bar{B}_{ind}\hat{C}$. Using the LV model, $\hat{C} = r/a$ (Table 1), we substitute in the body-mass-dependent version of $\bar{B}_{ind}$ (see above) and Eq. 1 to get the following:

$$B_{tot} \propto \frac{M_c^\mu M_r^{\rho+1}}{M_c^\varepsilon M_c^\alpha} \propto M_c^{\mu-\varepsilon-\alpha+\psi(\rho+1)}.$$

With parameter estimates, $B_{tot} \propto M_c^{-0.52}$ (95% CIs are -0.11 and -2.23; the asymmetry of the confidence intervals is presumably related to the specific manner in which the parameter distributions combine in the prediction). Because the confidence interval does not include zero, this result suggests that the pie-slicing model cannot correctly predict the size–density scaling of carnivores. In addition, the scaling slope for carnivores is steeper than would be expected from the pie-slicing model, but this steepness is accounted for in the dynamic approach.

Eq. 1 highlights the importance of prey size selection and searching or attack behavior of consumers in generating the scaling of abundance. It seems likely that, given the scaling of individual energetic demands, these traits are aspects of foraging behavior that must be linked. Presumably, organisms that attack large prey need to attack them less often, so that these factors should be negatively correlated, but we found that residuals of the two traits were not significantly correlated ($r = 0.36$, $P = 0.43$).

In many systems, consumers may be consumed by individuals in higher trophic levels, introducing additional factors that may influence size–density scaling (Blanchard et al. 2009). In this study, we focused on top-level consumers in order to simplify the problem and illustrate how size–density scaling arises. All of the models we considered used a natural mortality rate, but the effects of additional mortality on the consumer could be explored with tri-trophic models. However, the complexity of such models makes the analytical insights we generate here much harder to produce, but differences in slopes between upper and lower trophic levels suggest an important role for higher trophic levels in driving size–density scaling for many consumers (Blanchard et al. 2009).

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SUPPLEMENTAL MATERIAL

Appendix A

The scaling of consumer–resource model parameters (*Ecological Archives* E093-044-A1).

Appendix B

Details, sources, and fits for functional responses of mammalian carnivores (*Ecological Archives* E093-044-A2).

Supplement

Data for the functional response of five mammalian carnivores preying on mammals (*Ecological Archives* E093-044-S1).